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OBSERVATIONS AND REFLECTIONS

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APPENDAGES

AND ON

THE NERVOUS SYSTEM

OF

APUS CANCRIFORMIS.

BY

E. RAY LANKESTER, M.A., F.R.S.,
JODRELL PROFESSOR OF ZOOLOGY IN UNIVERSITY COLLEGE, LONDON.

Reprinted from the 'Quarterly Journal of Microscopical Science' for April, 1881.

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OBSERVATIONS *and* REFLECTIONS *on the* APPENDAGES *and on the* NERVOUS SYSTEM *of* APUS CANCRIFORMIS. By E. RAY LANKESTER, M.A., F.R.S., Jodrell Professor of Zoology in University College, London. (With Plate XX.)

APUS CANCRIFORMIS is in many respects one of the most important of the Crustacea. Not only is it of exceptionally large size for one of the Entomostraca, and therefore suited to anatomical investigation, but it possesses peculiarities of organisation which mark it out (together with its immediate congeners, the Phyllopoda) as an archaic form, probably standing nearer to the extinct ancestors of the Crustacea than any other living members of the group.

The almost world-wide distribution of the genus Apus (Greenland, Tasmania, New Zealand, Australia, Europe, North America, West Indies, Affghanistan, China), and its fresh-water habit, tend to confirm the conclusion as to its high antiquity.

But it is not only for such reasons that Apus has claims on our special attention. Its great abundance in certain localities renders it especially suitable for study as a type or standard of the organisation of the lower Crustacea, and it is on this account especially to be desired that an accurate account of its structure should be accessible. Strange as it appears, it is yet the fact that such an account does not exist, and that recent writers of authority have given divergent and erroneous accounts of such prominent features in the structure of Apus as the antennæ, jaws, and thoracic appendages.

In 1841 E. G. Zaddach published a memoir entitled 'De Apodis cancriformis anatome et historiâ evolutionis,' which is a most carefully worked out and admirably illustrated monograph, worthy to be placed alongside the similar studies of Arthropod anatomy, which were produced at about the same period by George Newport.

Zaddach's most valuable observations refer to the internal anatomy and to the development of Apus from the egg, but the problems relative to the morphology of the appendages and the reciprocal relationships of the great groups of Arthropoda which now occupy attention had not in 1841 come into prominence, and accordingly we do not find his observations upon the various appendages altogether equal in value to the rest of his work.

Since the date of Zaddach's monograph the only writers whom it is necessary to cite who have dealt with the structure of Apus are: Grube ("Bemerkungen über die Phyllopoden"), in the 'Archiv f. Naturg.,' 1853; Baird, in his 'British Entomostraca,' Ray Soc., 1850; Claus, in a paper published in the 'Gottingen Abhandlungen,' vol. xviii, 1873, entitled "Zur Kentniss des Baues und der Entwicklung von Branchipus stagnalis und Apus cancriformis;" Huxley, in his 'Anatomy of Invertebrate Animals,' 1877, p. 281; Gerstaecker, in Bronn's 'Classen und Ordnungen des Thierreichs,' "Crustacea," p. 860, &c., plates xxx, xxxii, 1879; and again, Claus, in the last edition (now in course of publication) of his 'Handbuch der Zoologie,' p. 527, 1880.

Having made a careful examination of the appendages of *Apus cancriformis,* of which I have received numerous specimens from the neighbourhood of Munich, from Prag, and from Padua, through the kindness of Professor von Siebold, of Professor Fricz, and of Professor Pavesi, respectively, as also of a specimen of *Apus Dukii* from Affghanistan, which I owe to the kindness of Surgeon-Major Day,[1] I was surprised to find that neither Zaddach nor any one of the authors above cited gives a full account of these structures. Moreover, I found my results to be at variance on one or more important points with the statements of each of my predecessors, who also differ from one another as to the interpretation of some portions of the series of limbs.

The most complete set of figures is that given by Professor Gerstaecker of the appendages of *Apus productus,* which are incorporated with reproductions of the figures of Zaddach, Claus, and Brauer,[2] in the plates of his valuable treatise on "Crustacea" (Bronn's 'Thierreich').

These original drawings, and the interpretation put upon them in the explanation to the plate, appear to me to be so inaccurate that I think that my sketches, reproduced in the plate (Plate XX) accompanying this paper, and the following observations, may be found of value as a contribution towards a true history of the "Krebsartige Kieferfuss" of Schaeffer.

DESCRIPTION OF THE APPENDAGES.

The modified limbs or lateral appendages of Apus may be divided into four series, according to their position, viz.—1.

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[1] This form, recently described by Mr. Day, is perhaps the *A. Himalayanus* cited in Gerstaecker's list.

[2] 'Sitzungsber. der Akad.,' Wien, Bd. lxix.

Two pairs in front of the mouth—"præoral appendages." 2. Three pairs of jaw-legs, more especially related to the purposes of the mouth as jaws, and immediately following it—"oral appendages." 3. Eleven pairs of variously modified but essentially locomotor legs, placed one on each of the eleven body segments, in front of and inclusive of the segment carrying the genital apertures—"thoracic appendages." 4. Fifty-two pairs of locomotor legs, gradually diminishing in size, and posterior to the genital apertures (less numerous in incompletely-grown specimens)—"abdominal appendages." They are more numerous than the annulations of the integument of this region of the body, which are only seventeen in number, but they correspond in number with the ganglionic enlargements of the nerve cord.[1] There are four annulations of the body posterior to these appendages, and devoid of a continuation of the nervous axis, as well as of appendages. A fifth post-pedal segment is perforated by the anus, and carries a pair of jointed setose appendages, which may or may not be equivalents of the legs of the anterior region.

The two pairs of appendages in front of the mouth.—Both these pairs of appendages are of small size—relatively very much smaller than they are in the newly-hatched larva. The second pair is much smaller than the first, although in the larva the reverse relation obtains. Moreover, the second pair, like the first, are simple filamentous tactile organs; although in the larva they are powerful biramose swimming legs. In the adult Apus, therefore, not only with reference to their homology with the corresponding appendages of the lobster, but also in view of their function, these two pairs of appendages are entitled to the names antennules (1st) and antennæ (2nd) respectively.

It appears to be desirable, in order to arrive at true conclusions with regard to the homologies of the limbs of the Arthropoda, to abandon altogether the use of such terms as "antenna," "mandible," and "maxillipede," as homological categories, and to apply them merely as descriptive terms proper to the particular case under examination. In the consideration of homologies the appendages should be regarded simply as first, second, third, and so forth, without the introduction of terms calculated by their reference to function to prejudice the argument as to homology. The first appendage of an Arthropod A. may be homologous with (or homogenous with) the first appendage or with the second or third of another Arthropod B., and so on; but ambiguity is inevitably introduced if we attempt to indicate this homology by the use of such terms as antennule and antenna, to be applied in both cases alike, for in such cases as the parasitic Copepoda, the various Arachnida, and the living and fossil branchiate scorpions (Merostomata), these descriptive terms, and others like them, are found to be absolutely contrary to fact in their implications, and involve also debatable assumptions in reference to ancestral primitive forms.

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[1] The first four post-genital body-rings carry five pairs of legs, the next four carry ten pairs of legs, the next four thirteen, the last five leg-bearing body-rings carry twenty four, as nearly as can be estimated.

The *first pair* of appendages of *Apus cancriformis* may, therefore, be described as functional antennæ. Each consists of two segments, separated by a joint or soft ring of the chitinous cuticle, which allows the bending of one joint upon the other; but there does not appear to be any muscular band entering the appendage in the adult Apus. A variable number (two to four) of setæ[1] are set upon the free end of the appendage.

The *second pair* of appendages is also antenniform. Each consists of a single filament, the base of which is attached to the under surface of the head, not far from the first. The filament is strongly curved but possesses no joint,[2] nor does any muscular fibre penetrate its axis. It tapers towards its free extremity which is setiform. Its total length is about one third of that of the first pair.

In the adult *Apus cancriformis* and in *Apus Dukii,* from Affghanistan (? *A. Himalayanus*), this second pair of præoral appendages, although reduced to a rudimentary condition, is always present, so far as my observations go. I have found them always present in full-grown specimens of *Apus cancriformis* from Munich, from Prag, and from Padua.

Their existence in the adult has recently been denied. Zaddach states that they are generally absent in *A. cancriformis,* but were found by him in two cases; Huxley states that he was unable to find them in *Apus glacialis* examined by him, whilst Claus, whose statements have the very greatest weight, both on account of his extended investigation of the morphology of the Crustacea and of his special observations on the development of Apus and Branchipus, brings forward the total absence of the second pair of præoral appendages in Apus as a special characteristic of the family Apusidæ. He says, in the fourth edition of his 'Grundzüge der Zoologie,' 1880, p. 527, "Die Tastantennen sind kurz zweigliedrige Fädchen, die hintern, welche bei der Larve einen zweiästigen Ruderarm bilden, fallen ganz aus." A similar statement occurs on p. 523. Gerstaecker offers no original observation on the subject, nor does he figure either the first or second pair of appendages of the *Apus productus*, which he has illustrated in his Pl. xxx, but confines himself to quoting the statement of Zaddach.

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[1] The setæ of Crustacea are in distinction from the bristles of Chætopods, which are also often called "setæ," superficial prolongations of the continuous chitinous cuticle which is produced by the epidermis, and are not, as are the bristles of Chætopoda, formed in open or closed follicles each as the cuticular excrescence of one specialised cell of the epiderm. It would be well to distinguish the follicle-formed setæ of Chætopoda as "chætæ" or "chætomes."

[2] A comparison with Zaddach's and Claus's figures of Apus larvæ leads to the conclusion that the part of the larval second antenna which thus survives is the base and short *proximal* ramus (neither exopodite nor endopodite); all beyond this forming the larger part of the larval antenna appears to atrophy completely.

The complete suppression of a pair of appendages is a matter of some importance, and in this particular case the presence or absence of the pair in question has a special interest in relation to the condition of that part of the nervous system by which they should be supplied. The fact is that, though rudimentary, the second pair of præoral appendages (so-called antennæ) is present in the adult Apus of at least two species.

Abdominal appendages: appendages behind the generative apertures.—It will be most convenient to pass next to the description of this group of appendages, since they appear to present the least specialised form of the whole series.

It has been customary to regard the higher Podophthalmata as a standard for the morphology of Crustacean appendages, and to interpret the parts seen in other Crustacea by reference to them, and to apply to those parts the analysis indicated in the terms protopodite (including coxopodite and basipodite), endopodite, exopodite, and epipodite. When, however, the question is looked at from the point of view of evolutional morphology, there appears to be no ground for expecting that the analysis applicable to the special adaptations of the Podophthalmata should also be applicable to the lower Crustacea, and it will be best to consider the parts of the appendages of Apus merely in reference to one another and to the appendages of closely allied forms, deferring for the present the consideration of the homologies or agreements of these parts with those of widely separated forms.

Taking the first post-genital appendage of the right side (seventeenth of the whole series), we find it to be a leaf-like plate attached by one end to the body, so that its flat surface is vertical to the ventral surface of the animal, and at right angles to the antero-posterior axis. It is provided with numerous lamelliform processes. The median portion may be spoken of as the axis or corm, whilst the processes may be called "phyllites" or "apophyses," those ranged along the ventral or neural border of the corm being called "endites," and those given off from the dorsal border being called "exites." There are six endites, and two exites much larger than any of the endites, whilst in front of (distal to) the two large exites is a less strongly marked outgrowth of the corm, which it will be convenient to call the "sub-apical lobe." The corm is devoid of segmentation or jointing,[1] its chitinous cuticle forming one continuous investment to it; and moreover, no muscles are inserted into the corm in such a way as to cause it to bend upon itself, and so call into existence functional, if not structural joints.[2]

The cuticle is thin at the base of the corm, where it becomes continuous with that of the ventral surface of the body, and the movement upon the joint so constituted is provided for by powerful muscles, which enter the appendage and are inserted into its walls.

Of the six *endites* the proximal is somewhat isolated and pushed towards the middle line. Its surface is beset with powerful setæ, and it clearly has the function of assisting, by means of apposition to its fellow of the opposite side, in seizing and moving particles which may be introduced into the mouth. It is a jaw process, and may be spoken of as the "*gnathobase.*" It is a fact of no little significance that a gnathobase is developed on every one of the sixty-three postoral appendages of Apus, especially when we remember that a similar feature is characteristic of Limulus, the most archaic representative of the Arachnida.

The gnathobase of the appendage under consideration is provided (as is the rule throughout the whole series) with powerful special muscles inserted into the corm (see figure), but it is not possible to define any arthrodial thinning of the cuticle which marks it off from the corm as a distinct segment.

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[1] Zaddach describes the corm as three-jointed, and Huxley states that in *Apus glacialus* it consists of coxopodite, basipodite, and ischiopodite. I cannot find any evidence of these joints in the specimens studied by me in any of the appendages excepting the first two of the thoracic series.

[2] Such functional joints not indicated by any thinning of the chitinous cuticle to form an arthrodial membrane appear to exist at the bases of many of the phyllites in limbs from various parts of the body, and are indicated by the insertions of the muscles in the appendages of various crustacean Nauplii, as well as in those of the remarkable Rotifer, Pedalion.

On account of its possessing muscles capable of moving it upon the corm, the gnathobase may be distinguished from such outgrowths of the corm as are devoid of muscles or not jointed at their base. Such outgrowths or apophyses probably are phylogenetically antecedent to outgrowths capable of flexion, or actually jointed at their base; accordingly, the simpler early condition may be indicated by the term "lobe," whilst the later flexible condition is indicated by the term "arthrite."

Mere lobes tend in various regions of the arthropod body to become arthrites, *e.g.* the spines on the abdominal carapace of Limulus, or, again, the carapace of some Entomostraca and the wings of insects.

Further, an arthrite may be monarthrous, or, as we shall see exemplified in other appendages of Apus, may become polyarthrous.

The four endites distal to the gnathobase are oval, leaf-like bodies, of which the proximal is somewhat broader than the others, and is, by exception in this and other appendages of the post-genital region, devoid of a special muscular slip, and therefore in the condition of a lobe instead of an arthrite. The three apophyses distal to it (3, 4, 5) are true arthrites, each being connected at its base with a muscular slip, which unites with its fellows to form a powerful muscle traversing the corm and inserted into the body wall. The arrangement of setæ on these endites is characteristic, and is best understood by reference to the figures.

The *distal endite* (6) is much larger than the preceding, and is attached at the point, which is practically the apex of the corm. It spreads both ventrally and dorsally from its point of attachment, so that a dorsal process may be distinguished from a ventral. It is provided with a muscle distinct from that of the other endites which traverses the corm.

Next in order we come to the *sub-apical lobe,* which may be regarded either as the termination of the axis of the corm or as the distal lobe of its external or dorsal border. In the appendage under description (the first post-genital), the subapical lobe is exceptionally large, but it is here as always a lobe—devoid of muscular supply, and not in any way jointed.

Passing midward along the dorsal border of the limb, we come to the largest of all the outgrowths of the corm—the *second exite* (counting the proximal as the first) the *flabellum* or *fan.*

It has been usual with authors to speak of this exite as a branchia, and to distinguish it from the next exite as the "lamelliform branchia," whilst the latter is termed the "bottle-shaped branchia." But the fact is, that it is possible with justice to attribute a respiratory function to any such broad lamelliform structure, although it may have other important functions. The flabellum is moved by three muscular slips arising from the corm, and is first of all a swimming or fanning plate. It is more highly developed as an "arthrite" than any other of the outgrowths of the corm. It is somewhat triangular in shape, attached by one angle to the corm, and has a setose margin.

The *proximal* or *first exite* is not really vesicular although frequently described as being so. It is somewhat thicker than the flabellum—oval in shape, with a very narrow and short pedicle, by which it is connected with the corm. It is devoid of setæ, and not provided with any muscles. It must be regarded as a "lobe" (in the sense above defined) rather than as an "arthrite." Throughout the series of limbs where present this proximal exite has much the same shape, it is always without setæ and is invariably devoid of muscular connections, although strongly emarginated and attached by but a slender neck to the corm. It can therefore have no locomotor function, and is, in virtue of negative qualities, *the* branchial outgrowth. On account of its passive character, as contrasted with the active fanning flabellum, it may be called the *bract* (bractea—a weather-cock).

In form the abdominal appendages which follow the first post-genital pair agree closely with the latter in all respects, except in the reduction of the relative size of the subapical lobe.

In size they undergo a gradual and very great reduction, so that the proportionate size of the last of the series is represented by the small fig. 13, of Pl. XX. The whole appendage is little bigger than the gnathobase of the first post-genital limb.

Gerstaecker's figure of the thirtieth truncal appendage in *Apus productus* (his Pl. xxx, fig. 10) appears to me to be inaccurate. These minute processes are easily mutilated in removing them from the body, and such has probably been the case with the appendage figured by him. The "flabellum" appears to have been broken away in Gerstaecker's specimen, and what he marks as flabellum (*br.*) is in reality the subapical lobe.

Abnormal appendage.—Any abnormality in a Crustacean appendage is of interest, as showing possible directions of new development or recurrence of ancestral conditions of form. In Pl. XX, fig. 12, an abnormal specimen of the fortieth appendage, right side, is drawn. The abnormality consists in the development of a second flabellum nearer the base of the corm than the first, and this is accompanied by an almost complete reduction of the bract. The additional flabellum is much smaller than the normal one, but has a similar form, and is supplied with a muscular slip.

Thoracic appendages, or appendages at and in front of the genital apertures and behind the specialised oral appendages.—It will be most convenient to examine these appendages by proceeding from behind forwards.

Oostegopods.—The pair which are attached to the segment in which the genital ducts open in female specimens of Apus are, as is well known, modified so as to form receptacles for the eggs. In the males, as shown by Brauer ('Wiener Sitzungsber,' vol. lxix), the appendages of this segment are in nowise different from those of the segments immediately in front of them.

The oostegopods, or brooding-legs (as the eleventh pair of the thoracic appendages may be called), present the following peculiarities as compared with the appendages in the region posterior to them. The gnathobase and four succeeding endites are normal (Pl. XX, fig. 10), and resemble those of the next posterior appendage (Pl. XX, fig. 11), but the sixth endite is greatly modified. It is expanded and confluent with the subapical lobe (*p*). The subapical lobe is widely produced in the form of a hemispherical cup. On to this expansion the flabellum (*Fl*) fits as a lid—an emarginated aperture being formed posteriorly to its short peduncle by the notching of its border (Pl. XX, fig. 10, *or*).

The great development of the subapical lobe and modification of the flabellum seems to have entailed an atrophy of the bract (*Br*), which exists in a rudimentary filamentous condition (compare the abnormal appendage drawn in fig. 12).

The general form of this appendage has been described by many previous observers, and the relations of its parts to those of neighbouring appendages correctly pointed out. The correspondence of the immovable, cup-like portion, developed from the axis or corm, with the conjoined sixth endite and subapical lobe (which is relatively large in the next following appendage posterior to it, fig. 11), has not, however, been insisted upon. Zaddach correctly identifies the movable lid with the flabellum, and figures the limb in an immature condition with the rudimentary bract present. He states that usually the rudimentary bract is absent in the full-grown condition, but I have, on the contrary, never failed to find it. Claus (loc. cit.) likewise figures this appendage from a larval Apus, and correctly identifies its component parts and the rudimentary bract which does not enter into the composition of the egg box. Huxley also (loc. cit.) describes the adult oostegopod, but without mentioning the rudimentary bract; he, however, identifies the movable lid as the flabellum (his "exopodite"), and the fixed cup-like portion as an outgrowth of the axis (his "endopodite"). Gerstaecker, however, having missed the rudimentary bract (which may or may not be present in the *Apus productus* figured by him), proceeds to identify the fixed portion of the egg box with the flabellum (his "lamelliform branchia"), and the movable lid with the bract (his vesicular (blasenförmiger) branchia). Gerstaecker's being the latest study and identification of these organs, it is of some importance to point out emphatically that the movable lid is not the bract, but the flabellum, whilst the bract exists in *Apus cancriformis* in a rudimentary condition in the adult appendage, as exhibited in Pl. XX, fig. 10.

I have not had an opportunity of examining, in the living state, the exact disposition of the muscles and the mechanism of the egg box, but I must point out that the circular muscles described by Zaddach have no existence. The modified flabellum alone has a muscular supply, which does not differ from that of the other flabella.

Appendages next in front of the oostegopods.—A marked difference in the proportions of the outgrowths of the limbs in front of the oostegopods is observed, as compared with those posterior to those specialised appendages.

In Pl. XX, fig. 9, the ninth of the thoracic (prægenital) series of foot-like appendages is represented. Whilst the gnathobase (endite 1) and the four next endites (2, 3, 4, 5) present no peculiarity for notice, the sixth endite is remarkable for its firmly chitinised walls, its denticulate ventral margin and its ex-axial lobe, which projects beyond the point at which the endite is articulated to the axis, and works in a notch of that portion of the limb.

The subapical lobe (*p*) is well developed and acutely angular. The flabellum is more elongated than in the abdominal (post-genital) appendages, being developed on either side of its point of attachment to the axis, instead of being quadrate or oblong. The two regions of the flabellum may conveniently be spoken of as "the distal lobe" (that apexwards in relation to the muscular attachment), and "the proximal lobe" (that basewards, in relation to the same attachment).

It is important to note this development, since in some Phyllopods and other Crustacea it is very greatly exaggerated, and the flabellum practically divided into two moieties (see woodcut, fig. 1, *XIX*, *XIV*, and *VI*, *F d*).

The muscles distributed to the endites and the flabellum are more strongly developed in the præ-genital than in the post-genital appendages of the locomotor series, as may be seen by comparing Pl. XX, fig. 9, with fig. 11. Whilst in the post-genital appendages endite 2 ceases to have a distinct muscular slip supplied to it, this endite, like all the others, has in the prægenital series a muscular slip from the great muscle of the axis, which is distributed to the five distal endites. The sixth endite has, in addition, a separate muscle, which runs parallel with the common muscle of the endites, and the first endite or gnathobase has also its own special muscles. The muscular supply of the sixth and first endites is the same in all the thoracic and abdominal appendages, excepting the first two of the thoracic series (two anterior thoracic feet of authors).

The bract is in all cases devoid of any muscular supply—a fact which is not without importance in the determination of its homologue in other Crustacea.

The appendages in front of the ninth of the thoracic series have a form closely similar to that drawn in Pl. XX, fig. 9, the endites becoming slightly more elongated in form, and the axis also elongated, so as to separate the endites from one another in those nearest the first two thoracic feet.

The first two thoracic feet require special description.

Second thoracic foot.—This appendage is drawn in Pl. XX, fig. 8. The most important feature which it presents, as distinguished from those behind it which have been already considered, is the jointing of the corm or axis. The corm is divided into two segments or pieces by a soft fold of its chitinous cuticle, and muscles are attached to the distal segment so as to move it upon the basal segment. To the basal segment (Ax^1) are attached the two proximal endites (en^1 and en^2), whilst the four distal endites, the flabellum and the bract, are attached to the distal segment (Ax^2). The endites are much elongated and notched at their margins, retaining, however, a flat or lamelliform character. The terminal endite (en^6) is strongly denticulate and has its ex-axial process markedly developed, whilst the notch in the axis into which this process fits is peculiarly constructed, as may be best understood from the figure (Pl. XX, fig. 8, *p* 2), and from the similar structure more definitely developed in the thoracic appendage (fig. 7 *a.*). I am not able to suggest what may be the significance of this lobe and notch, which has not been hitherto noticed by those who have described Apus, but it in some degree suggests a comparison with the peculiarly modified lobes on the first thoracic foot of the male *Limnetis brachyurus* (as described by Grube, Wiegmann's 'Archiv,' 1853).

The sub-apical lobe is relatively small, the flabellum and bract similar to those of hinder appendages.

First thoracic foot.—This appendage is more strikingly modified than any one of the locomotor series, excepting the oostegopods, the remarkable feature being the elongation and jointing of the four middle endites in the form of filamentous flagella. The axis or corm of this appendage is divided into four successive segments, which are marked in the figure respectively Ax^1, Ax^2, Ax^3, Ax^4 (Pl. XX, fig. 7). These segments are movable upon one another, the chitinous cuticle being soft so as to form an "arthrodial membrane" between the successive joints. This is the only one of the truncal series of appendages (those following the oral appendages) which presents four joints to the corm, whilst the second thoracic foot is the only other appendage of the truncal series which presents a joint in the corm at all and in it only two segments exist. A different structure is assigned by Professor Huxley to the corresponding limb and to the thoracic limbs generally of *Apus glacialis*, but it seems possible that the coxopodite, basipodite, ischiopodite and the endopodite with four joints recognised by him in that animal, are due to an interpretation of parts identical with those of *Apus cancriformis*, which differs from the interpretation here given. I must refer the reader for his views to the description and figures given on pp. 280, 281, of the 'Anatomy of Invertebrate Animals.'

The proximal or basal segment of the corm of the first thoracic limb of *Apus cancriformis* supports one endite, the gnathobase (En^1), which is quadrangular in outline and provided with strong setæ as in the other thoracic limbs. The second segment (Ax^2) supports a single endite, which is short and of filamentous form, with ten joints or annulations of the chitinous cuticle. These annulations in the present and other filamentous endites are not complete, but are developed only at the sides of the filament, leaving a continuous band of non-annulated chitinous cuticle mesially between the two series of half-rings; and moreover, the half-rings do not always coincide with one another in position, that is, are not exactly opposite to one another.

The third segment of the corm supports on its ventral margin one filamentous endite which has forty annulations or thereabouts. On its dorsal margin this segment gives attachment to the flabellum and the bract.

The fourth segment of the corm carries one long endite with fifty annulations (*end*^{4}) on its ventral margin, and terminally is produced into a non-movable process from which two endites arise, one (*end*^{5}) very long and filamentous with eighty annulations, the other (*end*^{6}) minute and boat-shaped, resembling the terminal endite (*end*^{6}) of other thoracic limbs. The peculiar shape of this terminal endite and the notch of the corm into which its exaxial process fits is shown in Pl. XX, fig. 7*a*.

It is at once obvious that in the first thoracic limb we have a very special differentiation of the endites in respect of their filamentous jointed form and of the corm in respect of its four movable segments. In both these features the second thoracic foot is intermediate between the first foot and those which follow posteriorly.

The first thoracic foot at once suggests comparison with some of the appendages of the Podophthalmatous Crustacea, as also with the limbs of Nauplius, but the discussion of the homologies of its parts with those of the limbs of other Crustacea, must be deferred to a subsequent section of this memoir.

The oral appendages.—The appendages immediately following the mouth constitute a natural group, which are distinguished by their small size and peculiar structure. I recognise three such pairs of appendages, a first (nearest the mouth), the mandibles (Pl. XX, fig. 3) ; a second, the maxillæ (figs. 4, 4 *a*, 5) ; a third, the maxillipedes (fig. 6). Very different interpretations have been placed upon these parts by different writers. Zaddach regarded the two pieces of the maxilla (figs. 4 and 5) as two distinct maxillæ—a first and second—in which view, with the curious difference that he transposes erroneously the natural position of the pieces, Gerstaecker follows him.

The maxillipede is described by Zaddach as a rudimentary thoracic foot—a view which is no doubt perfectly correct, though, on account of its relation to the oral series, it is more convenient to indicate it by the term maxillipede.

Grube agrees with Zaddach in regarding the two pieces of the maxilla as two distinct maxillæ, and the maxillipede as a rudimentary foot. Claus appears to have been the first to assign the two pieces of the maxilla to one appendage—a single maxilla—but causes some difficulty in arriving at a conclusion as to what he means by denoting the maxillipede (rudimentary foot of Zaddach and Grube) as the "second maxilla," without any explanation as to the difference between *his* second maxilla and Zaddach's. Huxley agrees with Claus in his statement, and characterises the second maxilla (my maxillipede) as foliaceous and almost rudimentary.

Mandibles.—These are figured in Pl. XX, figs. 3, 3 *a*. They appear to consist (according to Claus's observations on their development) of the basal portion of the corm of the larval appendage, which had at one time a form similar to that of the second præoral pair of appendages (woodcut fig. 1, *XVIII*).

Maxillæ.—The maxillæ (right and left) consist each of two plate-like pieces fitted closely together, one behind the other. The piece furthest from the mouth (which was described by Zaddach as the second maxilla and by Gerstaecker, through an oversight, as the first maxilla) seems to correspond to the gnathobase or proximal endite (en^1) of a thoracic foot. It is provided with numerous stout setæ (Pl. XX, fig. 5). The piece nearer the mouth (Zaddach's first maxilla, Gerstaecker's second) is in the form of a half-arch of chitinous substance, with a broad surface for the attachment of the other piece. It is provided with very numerous delicate setæ, which are arranged in the manner shown in the figures (Pl. XX, fig. 4), showing the aboral surface, and fig. 4 *a*, the adoral surface. The exact relation of the arch of the maxilla (as we may term the last described piece) to the gnathobase is not quite clear from the account given by Claus of the development, but it is quite certain that it is only a part of the same appendage as the latter.

Maxillipedes.—These appendages are of a very remarkable character. They have been universally recognised as *rudimentary,* not only on account of their small size (that drawn in Pl. XX, fig. 6, is on the same scale as that adopted for all the appendages), but also from the fact that they do not act as jaws on account of the wide separation of the right appendage from the left—whilst at the same time they are not fitted to be of much value as locomotor organs. They have not hitherto been correctly figured, the drawings of Zaddach and Grube being on a very small scale, whilst the drawing of Gerstaecker is out of all proportion in its exaggeration of the size relatively to that of other appendages, whilst the shape is incorrectly given.

A curious feature about these appendages is, that they resemble *bits* of a thoracic foot rather than a whole thoracic foot in a rudimentary condition. The corm or axis is utterly evanescent, a mere ridge (Pl. XX, fig. 6, *ax*). To this are attached two very well developed processes, one of which (*Br*) is clearly enough the bract, being identical in every respect with the bracts of the post-genital thoracic limbs. The other process is an oval chitinous plate, with long marginal setæ (en^1); it may possibly represent the flabellum, but more probably one of the endites, perhaps endite 1 (the gnathobase). There is no means of deciding this point, for Claus gives but a very slight allusion to the early condition of this appendage in his account of the development of Apus.

A highly important fact relative to this appendage was pointed out by Zaddach. Whilst a separate ganglion-pair of the ventral nerve-cord supplies the mandibles with nerves, and another distinct ganglion pair supplies the maxillæ, and another supplies the first thoracic foot, and a distinct ganglion pair is present for each of the succeeding pairs of thoracic feet, this pair of appendages *has no ganglion pair appropriated to it, but receives its nerves from the longitudinal cord* connecting the maxilla's ganglion pair with that of the first thoracic foot (woodcut, fig. 2, *V mp.*). It is important to observe that there is no evidence here of the fusion of two ganglion pairs and the consequent supply of two pairs of appendages from one and the same ganglion, but the nerves to the maxillipedes come off from the longitudinal commissure and not from a ganglion at all. In fact, we have evidence of the *total disappearance* of a ganglion pair corresponding to these rudimentary limbs.

Any facts tending to establish the occurrence of intercalation or of excalation of a segment (as represented by such structures as nerve ganglion-pairs and appendages) in the series building up the body of a Crustacean, Insect, or Arachnid is of great interest, since, if it be once admitted that a segment may disappear, or that a new segment may be introduced, the attempt to derive the series of segments and appendages of an Insect from those of a Crustacean or of an Arachnid, or of all three from a common ancestral form, loses all the difficulty which is encountered when the disappearance of segments is admitted as occurring *only* in the extreme posterior region, or only in that and the extreme anterior region of the series.

The maxillipedes of Apus appear to be rudimentary structures in the sense of structures which are degenerating and evanescent, not in the sense of structures which retain a primæval simplicity of form. In the course of the ancestral development of some other Phyllopoda (not in all), the corresponding appendages have entirely disappeared without leaving a trace behind them. It is well to bear in mind that were the maxillipedes of Apus a little further advanced in degeneration, so as to be devoid of the bract, and consist, like the "chilaria"[1] (metastoma) of Limulus, of simple setose chitinous plates, we should have no justification for calling them "appendages" at all, and they might very well, since no separate ganglion exists for them in the nerve-chain, although they receive each a nerve from the ventral nerve-cords, be regarded as median processes simulating rudimentary appendages. Such a view is very generally adopted with regard to processes termed "paragnathi" and "metastoma," and with regard to the "chilaria" of Limulus which last, like the maxillipedes of Apus, receive each a special nerve from the latero-ventral cords (woodcut, fig. 3, *chi*).

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[1] This useful term is introduced by Prof. Owen in his account of Limulus, 'Trans. Linnæan Soc.,' 1873.

Tabular enumeration of the Appendages of Apus cancriformis.

		Name adopted.		*Synonyms.*
Præoral appendages.		I, First antenna		Antennule: tactile antenna. First thoracic foot of Zaddach.
		II, Second antenna		Antenna: rowing-antenna. Second thoracic foot of Zaddach. Absent according to Claus.
		MOUTH		
Oral appendages.		III, Mandible		
		IV, Maxilla		First and second maxillæ of Zaddach, Grube, and Gerstaecker.
		V, Maxillipede		Second maxilla of Claus; third thoracic foot of Zaddach; rudimentary foot of Grube and Gerstaecker.
Truncal appendages.	Prægenital (Thoracic).	VI, 1st thoracic foot	(Eleven corresponding annulations of the body.)	Leg-like foot.
		VII, 2nd ,,		Swimming foot.
		VIII, 3rd ,,		,, ,,
		IX, 4th ,,		,, ,,
		X, 5th ,,		,, ,,
		XI, 6th ,,		,, ,,
		XII, 7th ,,		,, ,,
		XIII, 8th ,,		,, ,,
		XIV, 9th ,,		,, ,,
		XV, 10th ,,		,, ,,
		XVI, 11th ,,		Oostegopod in female, or brooding foot (Mutterfuss of Schaeffer).
	Postgenital (abdominal).	XVII, 1st abdominal foot	(Only seventeen corresponding annulations of the body.)	
		⋮ ⋮		
		LXVIII, 52nd abdominal foot.		

N.B.—The carapace is not attached to the segments posterior to that bearing the maxillipedes.

The last body-segment (thirty-third from the attachment of the carapace) has a pair of furcal processes, and is perforated by the anus.

The four body-segments in front of it carry no feet, the next two in front (28th and 29th of the segments of the trunk) have together as many as twelve pairs.

Explanation of Woodcut, Fig. 1.

In all the figures the endites are numbered from the basal one forward, as 1, 2, 3, 4, 5, 6. The proximal endites are often rudimentary or connate. In *II* and *III* endite 5 is suppressed, as becomes obvious on comparison with *IV*. *F* is the flabellum of the Apus limb, or its equivalent (*epipodite*); *p*, the sub-apical lobe; *B*, the bract; *B'*, a second bract in *XVII;* 5, the fifth endite or *endopodite;* 6, the sixth endite or *exopodite.*

I. First maxillipede of *Carcinus mænas* (after Boas, in 'Studier over Decapodernes Slœgtskabsforhold,' Kopenhagen, 1880).

II. Ditto of *Pagurus tuberculatus* (after Boas).

III. Ditto of Callianassa (after Boas).

IV. Ditto of Caridina (after Boas).

V. Second maxilla of *Astacus fluviatilis.*

VI. First maxillipede of ditto.

VII. Third maxillipede of ditto. 1, 2, rudimentary endites of the coxopodite; 3, 4, of the basipodite; 5, the ischiopodite or basal segment of the polyarthrous endopodite.

VIII. Second maxilla of Sergestes (after Claus).

IX. First maxillipede of ditto (after Claus).

X. Third abdominal foot of Palinurus (female), after Boas.

XI. Second maxilla of Zoea of Palæmonetes (after Boas).

XII. The same at the Mysis stage.

XIII. First maxillipede of same at the Mysis stage (compare with *XVI*).

XIV. Abdominal foot of Nebalia (after Claus), compare with *III* and with *X.*

XV. First rudiment of thoracic foot of Branchipus (after Claus).

XVI. Thoracic foot of larval Apus (after Claus).

X*VII.* Thoracic foot of *Branchipus Josephinæ,* after Grube.

XVIII. Second præoral appendage (second Nauplius' limb) of larval Apus.

XIX. Second thoracic foot of male Limnetis (after Grube).

Comparison of the appendages of Apus cancriformis with those of other Phyllopoda and of the Nauplius larva.—The appendages of the other species of Apus which have been described differ from those of *A. cancriformis* as to the number present in the post-genital or abdominal region. The length and the number of the joints in the filamentous endites of the first thoracic feet appear also to afford distinctive specific characters.

In other Phyllopoda the truncal appendages conform very closely to the plan of structure exhibited in Apus, presenting a corm with six endites, often a subapical lobe, and two exites. *Branchipus Josephinæ* of Grube (woodcut, fig. 1, *XVII*) is remarkable for possessing a third exite.

In the genera Branchipus, Artemia, Limnetis, Limnadia, and Estheria, the truncal appendages present special modifications of the constituent parts not shown in any part of the series in Apus, although the corresponding 'apophyses' are readily identified. One of the most remarkable modifications is seen in Limnetis, where the distal lobe of the flabellum becomes polyarthrous (woodcut, fig. 1, *XIX*, *d*). The interest of this modification consists in the fact that it lends some support to the identification of the flabellum of the Phyllopoda with the polyarthrous ramus termed 'exopodite' in the Decapoda. On other grounds I am led to doubt the correctness of this identification, as explained below. The fourth, fifth, and sixth endites in the same appendage of Limnetis are elongated, whilst the first, second, and third are short and jaw-like. The tendency of the flabellum to elongate itself in the direction parallel with the long axis of the corm is remarkable, and tends to its separation into a distal and a proximal lobe.

It is an important fact, which space does not allow me to further illustrate here, that the number of apophyses (both endites and exites), with the exceptional presence of an additional exite, is constant in the truncal appendages of all the Phyllopoda.

The præoral and oral appendages are very variously modified.

In order to determine further the homologies of the parts of the Crustacean limb it becomes important to ascertain what relation the parts of the foliaceous truncal appendages of the Phyllopoda have to the typical biramose appendages of a Nauplius.

The investigations of Zaddach, and more especially of Claus, on the development of Apus furnish data for this determination. The limbs present in the Nauplius larva of Apus and Branchipus persist in their primitive form at a time when the thoracic appendages have attained to a size nearly equal to theirs, and the comparison of the first and second thoracic foot (woodcut, fig. 1, *XVI*) with the biramose second pair of antennæ (same figure, *XVIII*) leaves little room for doubt as to the homologous parts. The Nauplius biramose appendage is devoid of flabellum and of bract; it has, in fact, no exites. Its terminal segment (outer ramus or exopodite) corresponds to the terminal endite of the thoracic foot (the sixth), and its inner ramus (endopodite) corresponds to the next endite of the thoracic foot or the fifth. Rudiments of two other endites are present in the second pair of Nauplian appendages of Apus.

The identification thus indicated is not capable of any more convincing proof than that afforded by the general similarity of relations in the two appendages compared; and when the extreme fluidity (if the expression may be used) or the Crustacean limb is borne in mind, and the undeniable tendency of one limb to become a pseudomorph of another, attaining *similar* form by identical modelling of parts *not* identical in origin, we have to be very careful in insisting upon conclusions arrived at by giving value to simple correspondence in form.

At the same time it appears most probable, and has been admitted by Claus and others, that the Nauplius appendages of Phyllopoda are devoid of flabellum and bract. Hence we may formulate the conclusion that the exopodite and endopodite of the Nauplius limb are homologous with the sixth and the fifth endites respectively of the thoracic limbs, and, similarly, that the flabellum is not homologous with the exopodite.

But when we come to examine the Nauplius of Decapoda (Penæus, &c.) we find that the exopodite of the second pair of Nauplian appendages becomes the short exopodite of the adult antennule, whilst the endopodite becomes the polyarthrous filament. Accordingly, if the exopodite and endopodite of the antenna of such a Decapod as Astacus are correctly identified with the parts called exopodite and endopodite (external and internal ramus) in the postoral series, the flabellum cannot be homologous with the exopodite of the maxillipedes and maxillæ. Such an homology might, however, be maintained by abandoning the current identification of the parts of the præoral and postoral appendages of Astacus. With regard to the antennules or first præorals of Astacus, there seems to be but little to justify the homology implied in calling its two rami respectively exopodite and endopodite, since in no Nauplius is this appendage biramose. Its distal segment in the Nauplius phase may with probability be identified with the external ramus (endite 6) of the antenna, but its inner ramus appears in Penæus at a late period, and may or may not be the equivalent of endite 5, the internal ramus of the antenna.

The drawing *XVI* in the woodcut, fig. 1, represents the form of all the thoracic appendages in the developing Apus (a younger condition is drawn in X*V*). It is interesting to note the extreme modification which the apophyses subsequently undergo in the case of the first thoracic foot. The flabellum and the bract expand, but the terminal endite becomes almost rudimentary and claw-like, whilst endite 5 grows out as a long polyarthrous filament, and endite 4 attains nearly the same length; endites 3 and 2 become shorter polyarthrous filaments, and endite 1 becomes the jaw process. On a first glance at the adult limb (Pl. XX, fig. 7) one would suppose that the long endites 5 and 4 were the parts homologous with the external and internal ramus respectively of the Nauplius limb; but the actual fact is that the reduced claw-like endite 6 is the homologue of the exopodite of the Nauplius antenna.

As has been pointed out above, the biramose antenna of the young Apus survives in the adult as a minute filamentous appendage, in which both endites 6 and 5 have atrophied, and only a portion of the axis and the small endite 1 (see woodcut, *XVIII*) persist.

The homologies of the parts of the appendages of some Malacostraca with those of Apus.—The attempt to establish a close correspondence between the apophyses of the appendages of the Phyllopoda and the Podophthalmata has its justification in the existence of the annectant form Nebalia, and of the Nauplius larval forms of some of the latter group. The foliaceous maxillæ and maxillipedes of such Decapods as Astacus also suggest a correspondence with the foliaceous truncal feet of Phyllopoda, which can be established in detail on close comparison.

If we take the second maxilla of Astacus to begin with (woodcut, *V*) we find it to consist of an unjointed corm with six endites, comparable to the six endites of the abdominal feet of Apus (Pl. XX, fig. 11).

The terminal endite is enlarged, and has a distal and a proximal lobe, as is more or less the case in the corresponding endite of the Apus limb. Two rudimentary exites (*p* in the woodcut) only are present, and in the adult are fused with the proximal lobe of the enlarged endite. In the Zoea phase of many Decapoda the enlarged endite is free in this region (woodcut, *VIII*), and in some cases the resemblance to a Phyllopod foot with suppressed flabellum and bract is very strong (woodcut, *IX*).

Passing to the next appendage of Astacus—the first maxillipede (woodcut, *VI*)—we can count the six endites as in the second maxilla, the sixth being greatly changed in form; instead of being a simple crescentic plate, it now has the shape of a rod, and is polyarthrous. But this change is no greater than that presented by the transition from the polyarthrous endites of the first thoracic limb of Apus to the lamelliform endites of the second and third limbs of that animal. A large exite is now present (*F*) with a small distal (*d*), and larger proximal lobe. It corresponds with the flabellum of the Apus limb and cannot be compared to the bract, owing to the fact that in this and subsequent appendages it has a muscular connection at its base and is richly setose on the surface, whereas, the bract of Apus is always devoid of muscular connection, and on its surface free from setæ. In fact, the bract of the limb of Apus appears to correspond, if with anything, in the limbs of Astacus and other Decapods, with branchial villi or lamellæ, and not with any of the large divisions of the limb. The corresponding maxillipede of a young Sergestes (*IX*) and of Palæmonetes (*XIII*) at the mysis-stage of development exhibit points of agreement with the Apus limb, which confirm the identifications just made in the case of Astacus. In Sergestes a subapical lobe (*p*) is present, whilst the resemblance of the Palæmonetes limb (*XIII*) to the young thoracic foot of Apus (*XVI*) is extraordinarily close. The flabellum in the two cases and the terminal endites 6 and 5 have practically identical form and relations respectively.

If we now take the third maxillipede of Astacus (*VII*) there is no difficulty in recognising the corresponding parts in it and the various appendages already noticed. In this appendage we have fully and clearly developed the apophyses which are, uniformly by modern writers, termed internal ramus or endopodite (5, *VII*); external ramus or exopodite (6, *VII*), and accessory ramus or epipodite (*F*, *VII*).

Accordingly it is now obvious that the endopodite of the Astacus maxillipede is the homologue of the endite 5 of the Apus limb, its exopodite is homologous with endite 6 of the Apus limb, and its epipodite is homologous with the flabellum of the Apus limb. This identification agrees with that arrived at in regard to the endopodite and exopodite of the antenna of Astacus as compared to the Apus limb through the intermediary of the Nauplius biramose appendage, and accordingly, it may be convenient to speak of the flabellum of the Phyllopod limb as the epipodite, the terminal endite as the exopodite, and the fifth endite as the endopodite. The two basal joints of the Astacus maxillipede constitute the corm, and are usually termed the protopodite collectively, the proximal joint being the "coxopodite" (*VII* 1, 2), and the distal the "basipodite" (*VII* 3, 4). These two pieces agree precisely in their relations to endites and exites with the two segments of the corm of the second thoracic foot of Apus (Pl. XX, fig. 8, Ax^1, Ax^2); on the other hand, the first thoracic foot of Apus (Pl. XX, fig. 7), shows each of the two pieces of the axis or corm in a further state of division. The four pieces of the corm of this limb have no similarly fourfold representative in the protopodite of any Decapod; and the two proximal *together* represent the coxopodite, and the two distal *together* represent the basipodite of the typical Decapod limb.

The homologies thus arrived at do not agree with those put forward by Professor Huxley in his 'Anatomy of Invertebrated Animals,' 1877, p. 281, since he identifies the flabellum of the Apus limb with the exopodite of Decapods, and regards the bract of Apus as representing the epipodite. Further, he considers a part of the corm or protopodite of the first thoracic foot of Apus as the endopodite, and the endites as merely secondary processes.

The careful examination, however, of the structure of the appendages of Apus leads, I think, when combined with the examination of the numerous modifications of the oral appendages of Decapoda, which recent writers have minutely described, to the conclusions which I have advanced above.

There are some further points of interest arising from the comparison of the walking and swimming feet of Malacostraca with the abdominal feet of Apus.

In those Decapoda in which, at an early period of their development, the maxillipedes and even the representatives of the ambulatory appendages resemble in form the biramose Nauplius limb (Sergestes, Penæus, and Schizopods) we obtain data for identifying the exopodite of the antenna with the exopodite of the postoral series, and similarly for identification of the endopodites. And thus by referring again to the Nauplius antenna of Apus and the assumed homologies of its part with the foliaceous limbs of the truncal region of that animal, we arrive by another method than that adopted when the comparison of the second maxilla of Decapods with the abdominal feet of Apus is made the starting point, at an identical determination of the homologies of the parts. The persistent ramus of the ambulatory limb of the Decapoda is the fifth endite of the Apus limb, its coxopodite and basipodite are the corm of the Apus limb, the sixth endite is suppressed as it so nearly is in the first thoracic foot of Apus—the epipodite is the flabellum, and the branchial plume, where present, probably represents the bract of the Phyllopod's appendage.

The relations of the thoracic swimming feet of Nebalia, and the abdominal swimming feet of Palinurus to the Apus limb—as they appear to me—are indicated by the letters affixed to those swimming feet in the woodcut (*XIV* and *X*).

A remarkably close agreement in form is seen when the first maxillipede of Callianassa (*III*) is compared with the lamelliform foot of Nebalia (*XIV*). But upon studying a series of first maxillipedes it becomes probable that the internal ramus (5) of Nebalia's swimming foot is *not* the same apophysis as that which forms the internal ramus of Callianassa's first maxillipede. For as shown by a comparison of the first maxillipedes of Carcinus (*I*) and of Caridina (*IV*), an apophysis (number 5) which is already much reduced in Caridina has altogether disappeared, both in Callianassa and in Pagurus (*II*).

This simulation of identical constitution by the thoracic foot of Nebalia and the maxillipede of Callianassa is an example of that 'pseudomorphism' which renders the determination of homologies of the parts of the Crustacean appendage in different regions and in different genera so difficult a problem.

The first maxillipede of Pagurus (woodcut, fig. 1, *II*) presents a feature which is of importance in relation to the determination of the parts present in the second maxilla of Astacus and allied forms. The second maxilla in the latter is destitute of any developed representative of the flabellum (epipodite); on the other hand, the first maxillipede *usually* in these Decapoda has a well developed flabellum. Pagurus, however, presents a first maxillipede, which, *like the second maxilla* of other Decapoda, is without any flabellum, and in connection with that absence we find a tendency of the sixth endite (exopodite) to become broad and flabelliform, as it is in the second maxilla. In Caridina (*IV*), a very small flabellum is present on the first maxillipede, and by its presence confirms the identification of parts adopted in regard to the first maxillipede of Pagurus.

THE CENTRAL NERVOUS SYSTEM OF APUS.

The remarkable condition of the central nervous system of Apus has been described and figured with great care by Zaddach, but whether his observations have been considered untrustworthy, or from whatever cause, no notice has been taken by recent writers of the very significant and exceptional disposition of the ganglia in the anterior region of the body which he brought to light. There is every reason for accepting the accuracy of Zaddach's observations, not only on account of the care which he appears to have given to this investigation, but because Grube described in 1853 (loc. cit.) a very similar but not quite identical disposition of the ganglia in *Limnetis brachyurus*.

In the Crustacea generally, the two pairs of præoral appendages receive their nerves from the præoral ganglion, which supplies also the eyes and the integument of the præoral region. On this account the two pairs of præoral appendages have been looked upon as being aboriginally appendages of the region in front of the mouth and in various other Arthropoda (*e.g.* the Arachnida and Limulus) the attempt has again and again been made to determine whether the first pair of appendages which are present in a given case are to be considered homologous with one of the præoral pairs of appendages of the Crustacea by an examination of the nerve-supply—it being held that if an appendage received its nerves from the præoral ganglion it would necessarily be the homologne of one of the similarly innervated præoral appendages of the Crustacea.

Anton Dohrn, for example, in discussing the affinities of Limulus, says: " Bei allen Krustern empfangen nämlich die beiden vorderen Extremitätenpaare ihre Nerven aus dem oberen Schlundganglion." And so firmly fixed is this conception with regard to the nerve supply of the two pairs of præoral appendages in Crustacea, that Dohrn has made it a subject of special remark that in certain Nauplius larvæ the first pair only (the antennules) receive their nerves from the præoral ganglion, whilst the second receive their nerves from the lateral cords, which pass posteriorly to form the ventral ganglionated cord.

Claus, who described this difference in the mode of nerve supply of the two præoral appendages of larval Phyllopoda, is led by it to a remarkable conclusion as to the nature of the two pairs of præoral appendages of Crustacea. He holds ('Grundzuge der Zoologie,' 3rd edition, p. 518) that *because* in these Nauplii the first pair of antennæ are supplied by the cerebral or præoral ganglion they are the equivalents of the antennæ or tactile appendages of the cephalic lobe of Chætopoda (Annelides); whilst the second pair of Nauplius appendages, or second pair of antennæ, are to be regarded as equivalents of postoral segmental appendages of Chætopoda, *because* they receive their nerves from the lateral cords and not from the præoral ganglion.

I have long been of the opinion which Prof. Claus appears to hold, that the appendages of the Arthropoda are homologous (or, to use a more distinctive term, " homogenous ") with the appendages of the Chætopoda, and on this account I consider it a proper step in classification to associate the Chætopoda with the Arthropoda and Rotifera in one large phylum, the Appendiculata (see "Notes on Embryology and Classification," this Journal, 1876, and Preface to the English translation of Gegenbaur's 'Elements of Comparative Anatomy').

At the same time I have not been led to conclude, as Prof. Claus does, that only one pair of the Crustacean antennæ are to be regarded as primarily postoral in position, and as representing the appendages of two originally postoral somites, but I think it probable that *both* antennæ are in this case, and that in the Crustacean there is no representative of the "antennæ" or tactile processes of the cephalic lobe of Chætopoda. Whilst this appears to me probable in regard to the Crustacea, it yet seems to me very possible that the antennæ of Peripatus and of Hexapod and Myriapod insects may represent true processes of the cephalic lobe or prostomium, as seen in Chætopoda.

In 1873, in the 'Annals and Mag. of Natural History' for May, p. 336, I said: "Much more likely, it seems, is the explanation that the oral aperture shifts position, and that the ophthalmic segment alone in Arthropoda represents the prostomium, the antennary and antennular segments being aboriginally metastomial, and only prostomial by later *adaptational shifting of the oral aperture.*" I was led to take this view by a consideration of the relations of the mouth to the appendages in Nauplius, and by the facts of the constitution of the head and its appendages in the Chætopoda.

Prof. Claus' removal of the second pair of antennæ from the præstomial to the metastomial region is based on a solid embryological fact as to the innervation of that appendage in the Nauplius, but it appears to me that the facts ascertained by Zaddach and Grube as to the structure of the nervous system and the supply of the appendages in certain adult Phyllopods—facts which were unknown to me in 1873—entirely confirm and establish on a firm basis the view that, in the Crustacea at least, the two præoral pairs of appendages are primitively postoral, and are neither of them related to the primitive prostomium or cephalic lobe, viz. the region innervated by the primitive cephalic ganglion, which ganglion I will venture, for want of a better name, to call the 'archi-cerebrum' of the Appendiculata.

The condition of things described and figured by Zaddach in *Apus cancriformis* is represented in the woodcut, fig. 2. The nerves to both pairs of antennæ are seen to arise, *not* from the quadrangular archi-cerebrum, but from the lateral cords at some distance from it, which are continued posteriorly to form the so-called 'ventral' nerve ganglion chain. A similar but less considerable separation of the nerves to the first pair of antennæ from the cerebral ganglion is described and figured by Grube in Limnetis ('Archiv für Naturgeschichte,' 1853).

In some very important respects the central nervous system of *Apus* appears to be more archaic and more nearly like that of the Chætopod annelids than is that of any other Crustaceans.

Recent researches on Planarians, Nemertines, Chætopoda, and Mollusca, point to the conclusion that the central nervous organs in all bilaterally symmetrical Cœlomata are primarily (or after a certain stage of evolution) a pair of *lateral* cords, consisting of nerve ganglion cells and nerve fibres, which are at first united to one another across the middle line only by commissural fibres. The more abundant nerve cells in the prostomial portions of these primitive nerve-cords form a pair of archi-cerebral ganglia, which unite with one another to constitute the primitive præstomial ganglion or archi-cerebrum. Meanwhile other ganglia or concentrations of nerve cells are formed upon the portions of the lateral cords lying behind the mouth, and these apparently correspond in number to the segments (if segments exist), which are differentiated in the metastomial axis. These metastomial ganglia may become highly specialised by the localising in them of all nerve cells, whilst the intermediate parts of the cords remain as simple bands of nerve fibres (Leeches, some Chætopods, most Arthropods, most Mollusca), or nerve cells may still occur in quantity between the ganglia (Peripatus, some Chætopods, Chitons). A distinct method of further change consists in the approximation to one another in the middle line of the two cords with their ganglia. This approximation may be slight, when it indicates an archaic condition (Peripatus, Serpula, &c.), or it may be so fully carried out that the ganglia, though rarely the cords themselves, are fused to one another in the middle line.

Apus is remarkable, as the woodcut (fig. 2) shows, for the wide divergence of its nerve cords in the first part of their course behind the mouth, and in this disposition confirms the conclusion (to which the isolation of its archi-cerebrum leads) as to its nervous system being preserved in a primæval or archaic condition.

It appears that, just as there is a tendency in the primarily lateral nerve ganglia of bilaterally symmetrical animals to move towards one another and fuse in the middle line of the body, so also there is another and similar tendency for primarily distinct and isolated ganglia to travel either backwards or forwards (usually forwards) along the lateral cords, *and*

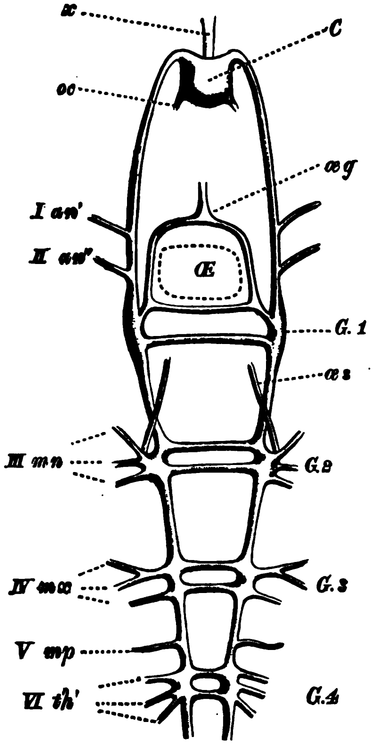

FIG. 2.—Diagram of the anterior portion of the nervous system of *Apus cancriformis* seen from below (constructed from Zaddach's figures).

C. Archi-cerebrum.
Œ. Œsophagus.
G. 1. First post-cerebral ganglion.
G. 2. Second post-cerebral ganglion (ganglion of the mandibular segment).
G. 3. Third post-cerebral ganglion (ganglion of the maxillary segment).
G. 4. Fourth post-cerebral ganglion (ganglion of the first thoracic segment).
I an'. Nerve to the first antenna.
II an''. Nerve to the second antenna.
III mn. Nerves to the mandible.
IV mx. Nerves to the maxilla.
V mp. Nerve to the maxillipede.
VI th'. Nerves to the first thoracic appendage.
x. Frontal nerves.
oc. Nerve to the left eye.
œg. Œsophageal ganglion impar.
œs. Posterior œsophageal nerve.

to fuse with neighbouring ganglia of the same side. This tendency is most obviously exhibited in the Mollusca, and in those animals affects more especially the part which has interest in connection with the morphology of Apus, namely, the adjacent præoral and postoral regions.

It is now well established that the archi-cerebrum (the primitive præstomial ganglion) of Gasteropods may, as it were, attract to itself ganglia developed originally at a distance from it, which were connected to it by nerve-cords, and may be described as running up these cords to fuse with the archi-cerebrum, and thus to constitute a complex cerebral ganglion, containing altogether new morphological elements. Such a process of complicating the præœsophageal ganglion pair is seen most obviously (to mention only one example) in the Nudibranchiata (Gegenbaur, English translation, p. 348), and a due appreciation of the possibilities of shifting and fusion of primarily distinct ganglia thus opened out affords the key to the very varied structure of the ganglion groups of the cephalous Mollusca.

Whilst, then, we distinguish the original ganglion pair of the præstomial region as the archi-cerebrum—it is well to designate by a distinct term the composite ganglion, which may result from the fusion with it of other ganglia—it may be called a syn-cerebrum.[1]

In the Chætopoda, the præ-œsophageal ganglion appears always to remain a pure *archi-cerebrum*. But in the Crustacea (and possibly all other Arthropoda, though there is a case to be considered for Peripatus and for the Hexapoda and Myriapoda, on the supposition that their antennæ are *not* the equivalents of Crustacean antennæ but of the processes of the cephalic lobe of Chætopoda) the præœsophageal ganglion is a *syn-cerebrum* consisting of the archi-cerebrum and of the ganglion masses appropriate to the first and second pair of appendages which were originally postoral, but have assumed a præoral position whilst carrying their ganglion masses up to the archi-cerebrum to fuse with it. This is true of all Crustacea, excepting Apus and possibly some other Phyllopods, and in possessing a widely isolated and pure archi-cerebrum (woodcut, fig. 2, C) Apus stands forward in a very marked position.

The only other case amongst adult Arthropods, in which it appears with certainty that the so-called cerebral ganglion is a pure archi-cerebrum, is that of Limulus.[2] Whilst some investigators have traced the nerves of the *two* first appendages of Limulus to the cerebral ganglion, and others have decided that only one (the first) pair derive their nerves from this ganglion—it appears from the admirable researches of M. Alphonse Milne-Edwards, that *none* of the appendages receive their nerves from the cerebral ganglion, but that it exists as a distinct emarginated mass of nervous matter, giving off nerves *only* to the simple and compound eyes and the frontal integument, as shown in the woodcut, fig. 3.

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[1] I am aware of the objection which may be taken to the compounding in these terms of Greek prefixes with Latin substantives, but I see no alternative.

[2] Balfour has shown that in spiders the ganglion of the cheliceræ is in

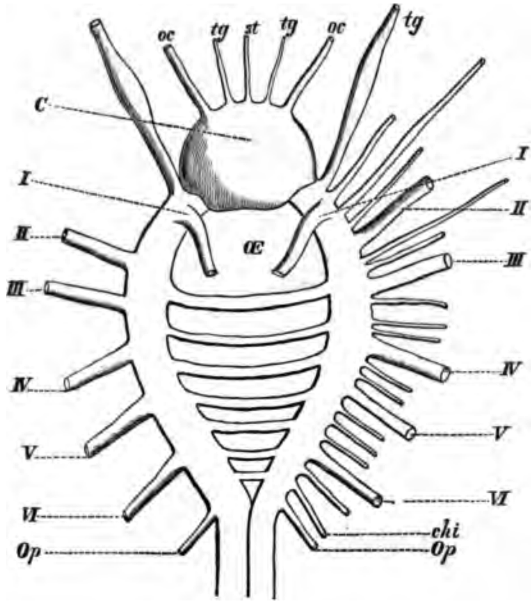

FIG. 3.—Diagram of the anterior portion of the nervous system of *Limulus polyphemus*, seen from below (schematized after Alphonse Milne-Edwards).

Œ. Position of œsophagus.
C. Archi-cerebrum.
oc. Nerves to the compound eyes.
tg. Frontal tegumentary nerves.
st. Nerve to the stemmata.
chi. Nerve to the chilaria (left side).
Op. Nerve to the operculum (left side).
I. Nerves of the cheliceræ or first pair of appendages.
II to *VI.* Nerves of the second, third, fourth, fifth, and sixth pairs of appendages.

An attempt has already been made to investigate the

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development postoral and distinct from the archi-cerebrum. This Journal, April, 1880.

intimate structure of the cerebral ganglion of Arthropods (*e.g.* of Astacus, of Blatta, and of Limulus). It appears to me that it will be of very great importance in this analysis to determine first of all the characteristic structure of the archi-cerebrum of Chætopoda, of Apus, and of Limulus, and then to advance to the composite syn-cerebra of the higher Crustacea, when it may be possible to distinguish as distinct morphological elements the nucleus furnished by the archi-cerebrum and the later accretions of primarily postoral ganglia. Possibly such a method of analysis may help in deciding whether the Hexapods' and Myriapods' antenna is a true outgrowth of the præstomial region (like the tactile processes of Chætopods) or a postoral appendage which has moved forwards.

Returning again to the woodcut diagram of the anterior portion of the nerve-cords of Apus (fig. 2), it will be observed that there are some other remarkable features besides the pure archi-cerebrum and the widely separated position of the lateral nerve-cords.

The nerves to the first and to the second antennæ come off from the lateral cord just in front of the elongated ganglionic swelling (*G* 1), which is joined to its fellow of the opposite side by two transverse commissures, as are the more posterior ganglia. A secondary œsophageal ring surrounding the dotted area of the œsophagus (*Œ*) is given off from the anterior of these transverse commissures, which are both post-œsophageal, and accordingly determine the ganglia (*G* 1) as post-œsophageal.

The question arises whether these elongated ganglia represent the fused ganglia of the antenna and antennæ. Possibly they do; in any case it is an altogether remarkable fact that there exists in Apus a pair of ganglia *behind* the œsophagus *in front* of the pair which are appropriate to the mandibles.

There is no such arrangement known in any other Crustacean excepting in Limnetis, where, according to Grube, there are actually *two* distinct pairs of ganglia in this position, the interior of which supplies the second pair of antennæ with nerves, whilst the first pair of antennæ are supplied from the lateral cords at the base of the cerebrum. On account of the small size of Limnetis some doubt may be entertained as to the complete accuracy of Grube's observations, but they tend very strongly to establish the general accuracy of those of Zaddach upon Apus[1].

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[1] I have not been able in my specimens of Apus, on account of their state of preservation, to make dissections of the nervous system; I should

It is quite possible that in Apus, owing to the diminutive size and rudimentary character of both pairs of antennæ, the ganglia appropriate to them have not fused with any others, but have entirely disappeared from the lateral cords. This possibility is forced upon the attention by the fact that the nerve to the maxillipedes comes off on each side from the lateral cord and has no ganglionic enlargement related to it (*V mp*). The mandibles and the maxillæ have, on the other hand, each a perfectly distinct, widely separate pair of ganglia (*G* 2 and *G* 3), the pairs being connected each by two transverse commissural strands. When the thoracic region is reached the nerve-cords approximate more closely to the middle line, but a distinct ganglion pair is developed for each pair of thoracic feet, of which the first only is seen in the figure (VI *th′*). Posteriorly, the ganglia are very closely set upon the cords, but, according to the statement of Zaddach, there is a distinct ganglion for each of the feet, even to the smallest of the abdominal (post-genital) series.

The facts as to the nervous system of Apus which I have above cited from Zaddach appear to deserve very serious attention, since they tend to show that the nervous system of Crustacea consists primarily of an archi-cerebrum and of two lateral cords, and that on each cord is a ganglion corresponding to each appendage; that the cords tend to meet one another in the middle line; that when appendages become rudimentary (*e.g.* the maxillipedes) their ganglia may disappear; that the first postoral ganglion pair is not in all cases that of the mandibles; and finally, that the nerves of the two first pairs of appendages are, in certain thoroughly typical Crustacea, given off from the lateral cords at a point far removed from the archi-cerebrum.

Whether the ganglion (*G* 1) has any relation to the nerves of the first and second antennæ might possibly be determined by a microscopical examination of the roots of those nerves.

In the course of the foregoing pages I have alluded to some points of resemblance between Apus and Limulus, the most important being the jaw-processes at the base of all the ambulatory limbs, and the presence of a pure archi-cerebrum in both genera.

I should wish, however, to guard against the inference that I consider any close affinity to obtain between Apus and Limulus. Apus appears to me to be an archaic Crustacean, and Limulus an archaic Arachnidan (not merely

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therefore be very grateful to any naturalist who would send to me by post perfectly fresh living examples of Apus.

"related to" the Arachnida, but definitely to be classed in that group). The points in which they agree are probably points in which they both approach the common ancestor of the Arachnida and Crustacea—but each of them presents clearly and definitely the dominant and distinctive structural attributes of its own class or branch of the pedigree of those Appendiculata which have appendages modified to serve as jaws—namely, the Arthropods or, better, Gnathopods.

EXPLANATION OF PLATE XX,

Illustrating Professor Ray Lankester's memoir on the "Appendages and Nervous System of *Apus cancriformis*."

In all the figures the following letters have the significance here attached to them:

Ax. Axis or corm (Protopodite) of the appendage.

Ax^1 to Ax^4. First, second, third, and fourth segments of the corm.

Ax^1 and Ax^2, in Fig. 7, are the equivalents of Ax^1 in Fig. 8; and Ax^3 and Ax^4 in Fig. 7 of Ax^2 in Fig. 8.

Ax^1, in Fig. 7, is the equivalent of the Coxopodite of higher Crustacea.

Ax^2, in Fig 7, is the equivalent of the Basipodite of higher Crustacea.

En^1. Proximal endite (proximal ventral apophysis) or gnathobase.

En^2. Second endite, or second ventral apophysis.

En^3. Third endite, or third ventral apophysis.

En^4. Fourth ditto.

En^5. Fifth ditto, the Endopodite.

En^6. Sixth ditto, the Exopodite.

P. Sub-apical lobe of the corm.

Fl. Distal exite (dorsal apophysis), or flabellum (Epipodite).

Br. Proximal exite, or bract (branchia).

N.B.—All the figures are drawn to the same scale, excepting Figs. 1 *a*. 7 *a*, and 14, and all the appendages are those of the right side seen from the posterior face, except Figs. 3 *a* and 4 *a*. The plumose character of the finer setæ is not rendered, except in Figs. 6 and 13.

Fig. 1.—First præoral appendage, or first antenna.

Fig. 1 *a*.—Enlarged view of the termination of another specimen with four terminal setæ.

Fig. 2.—Second præoral appendage, or second antenna.

Fig. 3.—Mandible.

Fig. 3 *a*.—Mandible revolved on its long axis (anterior face).

Fig. 4.—Maxilla anterior piece.

Fig. 4 *a*.—The same piece reversed (anterior face).

Fig. 5.—Maxilla posterior piece (gnathobase).

Fig. 6.—Maxillipede.

Fig. 7.—First thoracic foot.

Fig. 7*a*.—Enlarged view of the sixth endite of the first thoracic foot.

Fig. 8.—Second thoracic foot.

Fig. 9.—Seventh thoracic foot.

Fig. 10.—Eleventh thoracic foot (oostegopod).

Fig. 11.—First abdominal (post-genital) foot.

Fig. 12.—Abnormal thirtieth abdominal foot, with two flabella and rudimentary bract. Fl^2. Second or additional flabellum.

Fig. 13.—Fifty-second abdominal, or sixty-third truncal foot (sixty-sixth post-oral appendage, sixty-eighth or last appendage of the entire series).

Fig. 14.—Setæ from the apophyses: *a* and *b*, lateral and full views of the short setæ on the endites 2 to 5 of the appendages, drawn in Figs. 9, 10, and 11; *c*, longer setæ from the gnathobase of the maxillipedes and the margin of the sub-apical lobe and flabellum.

[illegible]